Vegetation, soils, and forest productivity in selected forest types in interior Alaska

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Vegetation, forest productivity, and soils of 23 forest stands in the taiga of interior Alaska are described. The stands are arranged on an environmental gradient from an aspen (*Populus tremuloides* Michx.) stand on a dry, steep south-facing bluff, to open black spruce (*Picea mariana* (Mill.) B.S.P.) stands underlain by permafrost on north-facing slopes. The coldest site is a mixed white spruce (*Picea glauca* (Moench) Voss) and black spruce woodland at the treeline. Mesic upland sites are represented by successional stands of paper birch (*Betula papyrifera* Marsh.) and aspen, and highly productive stands of white spruce. Several floodplain stands represent the successional sequence from productive balsam poplar (*Populus balsamifera* L.) and white spruce to black spruce stands underlain by permafrost on the older terraces. The environmental gradient is described by using two soil factors: soil moisture and annual accumulated soil degree days (SDD), which range from 2217 SDD for the warmest aspen stand to 480 SDD for the coldest permafrost-dominated black spruce site. Soils vary from Alfic Cryochrepts on most of the mesic sites to Histic Pergelic Cryochrepts on the colder sites underlain by permafrost. A typical soil profile is described for each major forest type. A black spruce stand on permafrost has the lowest tree standing crop (1586 $g \cdot m^{-2}$) and annual productivity (56 $g \cdot m^{-2} \cdot year^{-1}$) whereas a mature white spruce stand has the largest tree standing crop (24 577 $g \cdot m^{-2}$) and an annual productivity of 540 $g \cdot m^{-2} \cdot year^{-1}$, but the successional balsam poplar stand on flood plain alluvium has the highest annual tree increment (952 $g \cdot m^{-2} \cdot year^{-1}$). The study supports the hypothesis that black spruce is a nutrient poor, unproductive forest type and that its low productivity is primarily the result of low soil temperature and high soil moisture.

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L'article traite des sols, de la végétation et de la productivité de vingt-trois peuplements forestiers de la taïga de l'intérieur de l'Alaska. Les peuplements sont répartis selon un gradient stationnel allant d'un peuplement de *Populus tremuloides* Michx. sur falaise à exposition sud, jusqu'à des peuplements ouverts de *Picea mariana* (Mill.) B.S.P. sur pergélisols de versants exposés au nord. Le peuplement de la station la plus froide est constitué d'un mélange de *Picea glauca* (Moench) Voss et de *Picea mariana*, à la limite des arbres. Les stations mésiques bien drainées sont représentées par des peuplements de succession de *Betula papyrifera* Marsh. et *Populus tremuloides*, et des peuplements très productifs de *Picea glauca*. Plusieurs peuplements sur plaine alluviale représentent la série allant de peuplements productifs de *Populus balsamifera* L. et *Picea glauca* à des peuplements de *Picea glauca* et *Picea mariana* sur pergélisols des terraces les plus anciennes. Le gradient environnemental est décrit par l'emploi de deux facteurs édaphiques: l'humidité du sol et le nombre de degrés jours annuels du sol; ce dernier varie de 2217 DJS pour la station la plus chaude, de *Populus tremuloides*, à 480 DJS pour la station la plus froide, de *Picea mariana* sur pergélisol. Les sols varient depuis les Cryochrepts Alfic, sur la majorité des stations mésiques, aux Cryochrepts Histic Pergelic des stations les plus froides sur pergélisols. Un profil de sol typique est décrit pour chaque type majeur de forêt. Les plus faibles valeurs de population sur pied (1586 $g \cdot m^{-2}$) et de productivité (56 $g \cdot m^{-2} \cdot an^{-1}$) sont celles d'un peuplement de *Picea mariana* sur pergélisol, alors que la plus grande population sur pied (24 577 $g \cdot m^{-2}$) et la production la plus élevée (540 $g \cdot m^{-2} \cdot an^{-1}$) sont pour un peuplement mûr de *Picea glauca*; c'est toutefois le peuplement de *Populus balsamea* sur plaine d'alluvion qui présente l'accroissement annuel le plus élevé (952 $g \cdot m^{-2} \cdot an^{-1}$). Cette étude appuie l'hypothèse voulant que les peuplements de *Picea mariana* sont associés à des stations pauvres et que leur faible productivité résulte surtout de la basse température et du haut niveau d'humidité du sol.

[Traduit par le journal]

Introduction

The taiga in interior Alaska is a mosaic of vegetation types resulting primarily from past fires and the characteristics of slope, aspect, elevation, drainage, and parent material. In this paper we describe the forest vegetation, soils, and ecosystem parameters along a wide

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environmental gradient.

In the Fairbanks area, upland forest types vary from highly productive aspen (*Populus tremuloides* Michx.), birch (*Betula papyrifera* Marsh.), and white spruce (*Picea glauca* (Moench) Voss) stands on south-facing, well-drained slopes, to permafrost and moss-dominated black spruce (*Picea mariana* (Mill.) B.S.P.) forests of low productivity on north-facing slopes (Viereck 1975). Floodplain forests of balsam poplar (*Populus balsamifera* L.) and white spruce are productive on recently formed river alluvium where permafrost is absent, but slow-growing black spruce and bogs occupy the older terraces which are underlain by permafrost. Permafrost underlies as much as 75−80% of the area, including almost all terrain except south-facing slopes and floodplains adjacent to major rivers. Black spruce is the most widespread forest type, covering 44% of the area and usually associated with permafrost. Treeline forests characterized by open stands of black and white spruce occur at about 750 m on the surrounding hills. In general the forest sites can be divided into cold, wet, black spruce sites usually underlain by permafrost, and mesic white spruce sites, and successional stages leading to white spruce, on warm, well-drained, permafrost-free soils.

The climate of the area is strongly continental; temperature extremes range from −50 to +35°C. The mean annual temperature is −3.5°C. January is the coldest month with an average temperature of −25°C, and July is the warmest with an average temperature of +16°C. Air temperature degree day summations based on 5°C are 1076 degree days for the 30-year average of Fairbanks. During our study, totals ranged from 1400 degree days for the warmest site to 500 for the treeline site. The average annual precipitation is 286 mm, with about 30% falling as snow. Monthly precipitation is low during spring and early summer but increases in late summer to a maximum of 58 mm in August. According to Thornthwaite's classification, the climate in the Fairbanks area is semiarid (Patric and Black 1968).

Because of the cold and dry climate, which reduces the intensity of chemical weathering, soils have slight morphological development. Inceptisols, Entisols, and Histosols occupy 78, 12, and 7% of the land area. Throughout the Fairbanks region, silt loam upland soils have developed from loess that originated from extensive glacial outwash streams that were prevalent during the last glacial maximum. Floodplain soils have developed in sandy or silt-textured alluvium.

When the study of a black spruce ecosystem was developed at the Washington Creek Fire Ecology Research Area (Van Cleve, Dyrness et al. 1983) it was recognized that the intensive site with its black spruce − permafrost ecosystem was near the extreme end of the continuum in terms of forest productivity, mineral cycling, and controlling variables, such as soil temperatures, but that to thoroughly understand the black spruce ecosystem, we needed to compare it with other more productive and less productive forest sites. To test various hypotheses developed at the intensive site, we needed to have a number of semi-intensive sites established over as wide an environmental gradient as existed in the area. We also recognized that these sites should include forest stands where information had previously been gathered as part of other studies. We felt that these semi-intensive sites would be especially useful in testing hypotheses related to soil temperature, nutrient cycling, and forest productivity.

Study sites

In this paper information is presented from 21 widely scattered sites, which we designate as semi-intensive sites in this and other papers, and two transects at the intensive site. These sites, all within 50 km of Fairbanks (Fig. 1), were subjectively selected to represent a spectrum from the coldest sites at the treeline and on north-facing slopes, to the warmest and driest sites that support tree growth. Stands for which data were available from previous studies were selected whenever possible. The stands were classified according to Viereck and Dyrness (1980).

In the upland the warmest, driest south-facing site is represented by an aspen/*Shepherdia*/grass stand on a south-facing bluff above the Tanana River. A young aspen stand and two birch stands represent the deciduous forest stage after a fire on productive upland sites. A 165-year-old white spruce stand represents a later stage in this successional sequence.

Open and closed stands of black spruce with feather mosses or sphagnum, most of which are underlain by permafrost, are representative of the colder upland sites. The coldest site is a white spruce − black spruce/alder−shrub−birch/feathermoss type at an elevation of 750 m. The series of floodplain stands represents mid- to late stages of a successional sequence developing on newly exposed silt on both the Chena and Tanana rivers. Younger forest stages include 40-, 50-, and 100-year-old balsam poplar stands. The mature, productive white spruce stands include two 110- to 120-year-old stands and one 250-year-old stand. Older stages on terraces underlain by permafrost include a mixed black and white spruce stand and three black spruce stands. This successional sequence is described in detail by Van Cleve and Viereck (1981). The relative position of these stands along a cross section of the floodplains and uplands is shown in Fig. 2 and their geographic location is shown in Fig. 1.

The semi-intensive sites (numbered as stands 11 through 32 with no 17) and the intensive site (stands 33 and 34) are described below. Tree and vegetation data for each stand are given in Tables 1 and 2, and landform and soil information are given in Table 3. Biomass, annual tree productivity, and litter fall are given for only 16 of the stands (Table 4). In Tables 1 and 2 the stands are arranged by their position along an environmental gradient rather than in numerical order.

Methods

Vegetation

The vegetation was sampled by use of one fixed grid of 20

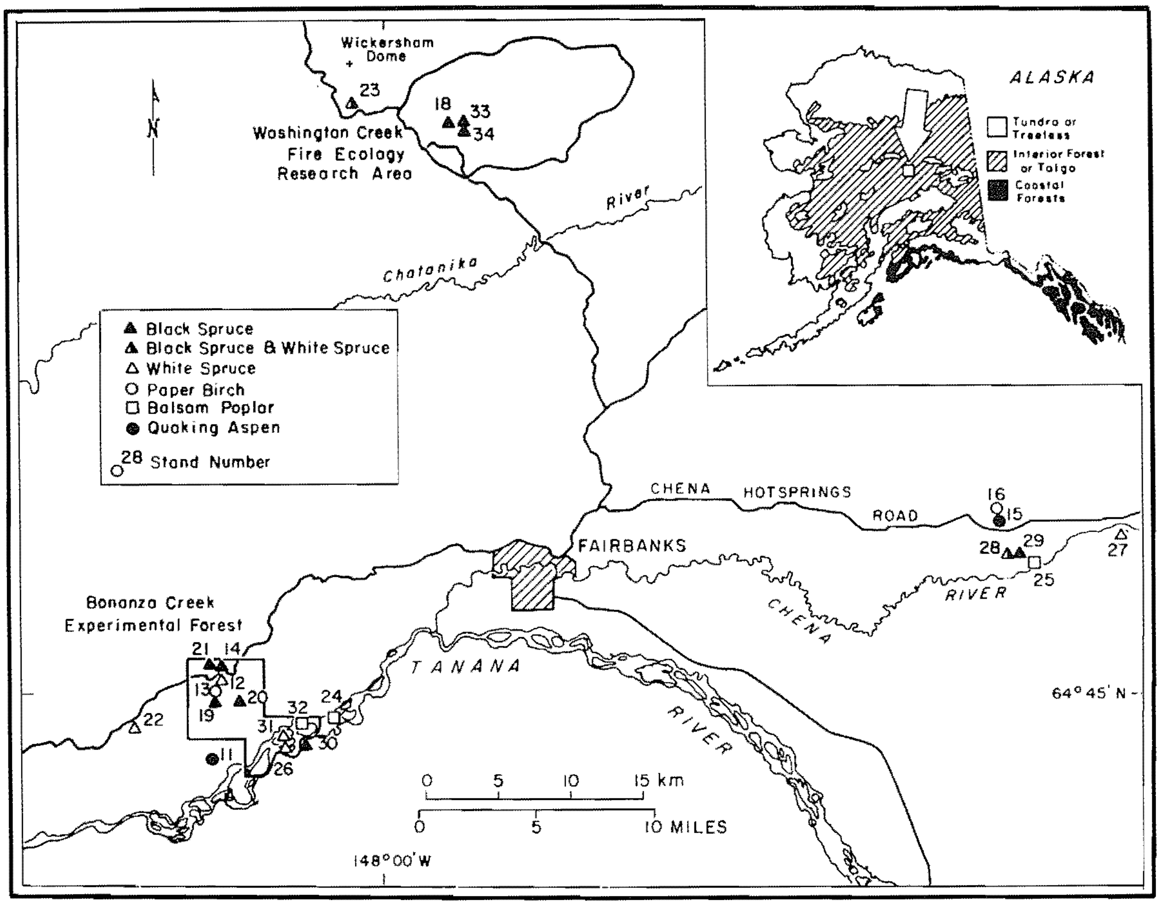

FIG. 1. Location of 21 semi-intensive sites (stands 11–16 and 18–32) and the intensive site (stands 33 and 34) in the Fairbanks area of interior Alaska.

points in each stand. At each point percent cover of herbs, low shrubs, mosses, and lichens was determined for a 1-m^2 plot; for seedlings and shrubs, a 4-m^2 plot was used; trees and saplings (under 2.5 cm diameter at breast height (dbh)) were sampled by the point quarter method, modified from Ohman and Ream (1971) and described in detail in Foote (1983).

Details concerning sampling for tree biomass annual tree production, element requirement, and litter fall are presented by Van Cleve, Oliver et al. (1983).

Soils

Two soil profiles were randomly selected and described at each site following procedures outlined in the Soil Survey Manual (Anonymous 1951). Samples from all important horizons were analyzed for pH and nutrients at the Forest Soils Laboratory, University of Alaska, following procedures discussed in Van Cleve et al. (1971). Soil taxonomy follows Furbush and Schoephorster (1977).

Microclimate

Soil temperatures were taken during the summer at 5, 10, and 20 cm at most of the stands. At the intensive site (stands 33 and 34) and stands 11, 12, 13, and 14 in Bonanza Creek Experimental Forest, soil temperatures were recorded continuously. At other stands temperatures were recorded weekly by the use of a thermistor probe or with thermistors permanently placed in the soil. The base of the living moss layer was used as the surface for determining depths. Soil degree days accumulations were calculated for the 10 cm depth, with 0°C as the base, and for the period May 20 to September 10. Depth to permafrost (the thickness of the active layer) was determined in late summer with a steel probe. Moisture content of the forest floor and surface 10 cm of mineral soil were determined by taking 15-cm-diameter cores of the forest floor and the upper mineral soil weekly and determining moisture content gravimetrically. Organic matter and soil samples were dried to constant weights at 65 and 105°C, respectively. Average soil moisture for the summer was determined for the period May 20 to September 10.

Descriptions of forest types and stands

Closed and open deciduous forest: aspen

Two aspen communities were included as study sites. One, on a south-facing bluff, represents the driest site conditions for tree growth in interior Alaska. The second, an upland south-facing gentle slope, represents

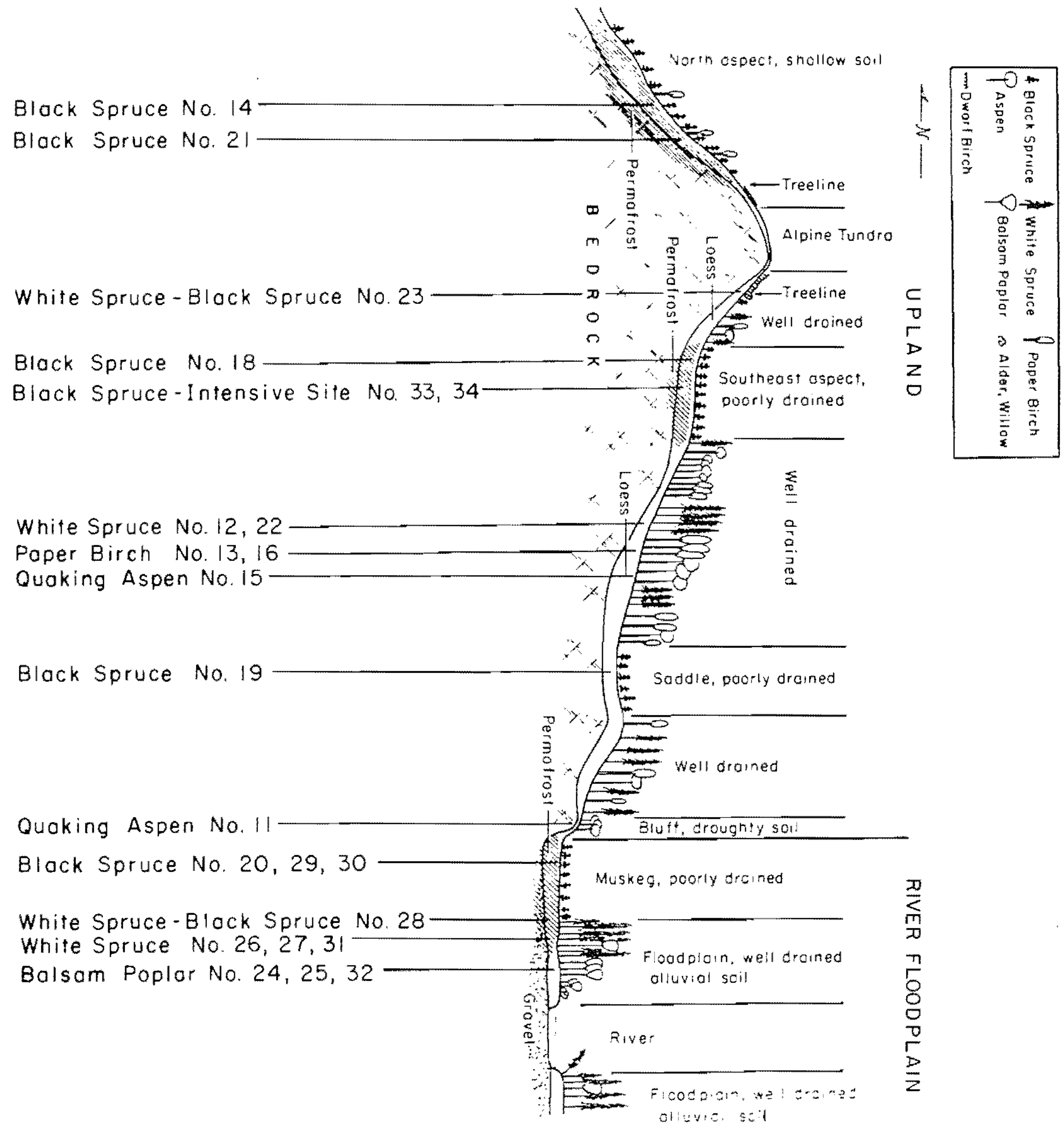

FIG. 2. Generalized cross section of topography, landforms, vegetation, and parent material in the Fairbanks area with locations of the semi-intensive sites (stands 11–16 and 18–32) and the intensive site (stands 33 and 34).

more mesic conditions, typical for aspen stands in interior Alaska. Both stands are young, 50–60 years old. Trees on the dry site average 6.7 cm in diameter and 10 m in height, whereas those on the moderate site average 11.9 cm in diameter and 20 m in height. The mesic site is more productive with a basal area of 30.1 $m^2 \cdot ha^{-1}$ compared with 8.7 $m^2 \cdot ha^{-1}$ for the dry site. The productivity is about twice as great in this mesic site, 760 $g \cdot m^{-2} \cdot year^{-1}$ compared with 363 $g \cdot m^{-2} \cdot year^{-1}$ for the dry site. Aboveground tree biomass is 4653 $g \cdot m^{-2}$ on the dry site compared with 17 490 $g \cdot m^{-2}$ on the mesic site. Litter fall ranges from 27 $g \cdot m^{-2} \cdot year^{-1}$ to 222 $g \cdot m^{-2} \cdot year^{-1}$ in the two stands, respectively (Table 4).

There is little similarity in the understory of the two stands: *Viburnum edule* (Michx.) Raf. and *Rosa acicularis* Lindl. are the dominant shrub in the mesic stand, and *Shepherdia canadensis* (L.) Nutt. and *Arctostaphylos uva-ursi* (L.) Spreng. dominate the dry aspen stand. In the mesic site herbs are scarce, but in the dry site a number of herbaceous species, especially *Calamagrostis purpurascens* R. Br., *Galium boreale*

TABLE 1. Tree, sapling, and seedling information for 23 forest stands in interior Alaska. Stands are arranged along an environmental gradient from warm and dry (at left) to cold and wet (at right)[a]

	Quaking aspen		Paper birch		Balsam poplar community			White spruce				White and black spruce			Black spruce								
	Populus tremuloides/ Shepherdia canadensis/ Calamagrostis purpurascens	*Populus tremuloides/ Viburnum edule/ Linnaea borealis*	*Betula papyrifera/ Alnus crispa/ Calamagrostis canadensis*	*Betula papyrifera/ Alnus crispa/ Calamagrostis canadensis*	*Populus balsamifera/ Alnus–Rosa/ Equisetum*	*Populus balsamifera/ Alnus–Rosa/ Equisetum*	*Populus balsamifera/ Alnus–Rosa/ Equisetum*	*Picea glauca/ Rosa acicularis/ Rhytidiadelphus triquetrus*	*Picea glauca/ Rosa acicularis/ Linnaea borealis – Hylocomium splendens*	*Picea glauca/ Hylocomium splendens*	*Picea glauca/ Rosa acicularis – Viburnum edule*	*Picea glauca/ Rosa acicularis – Viburnum edule/ Linnaea borealis – Hylocomium splendens*	*Picea glauca – Picea mariana/ Alnus crispa/ Rhytidiadelphus triquetrus*	*Picea glauca – Picea mariana/ Alnus crispa – Betula glandulosa/ Pleurozium schreberi*	*Picea mariana/ Ledum groenlandicum/ Hylocomium splendens*	*Picea mariana/ Vaccinium vitis-idaea –* feathermoss	*Picea mariana/ Vaccinium uliginosum/ Pleurozium schreberi*	*Picea mariana/* feathermoss	*Picea mariana/ Ledum groenlandicum/ Pleurozium schreberi*	*Picea mariana/* feathermoss	*Picea mariana/* (feathermoss– *Cladonia*)– (*Sphagnum*)	*Picea mariana/ Salix/Ledum/ Sphagnum*	*Picea mariana/ Ledum groenlandicum – Sphagnum*
Stand No.	11	15	16	13	32	25	24	27	26	12	22	31	28	23	30	21	18	19	20	33	34	29	14
Age of stand	50	60	60	130	50	60	100	130	115	165	70	250	230	110	150	60	70	130	60	140	120	130	145
Populus tremuloides																							
Tree density (no. · ha^{-1})	2445	1891	683								553												
Tree basal area ($m^2 \cdot ha^{-1}$)	8.7	21.0	7.9								13.5												
Tree height (m)	10	20	15								15												
Tree diameter (cm)	6.7	11.9	12.1								17.7												
Sapling density (no. · ha^{-1})	33		13																				
Seedling density (no. · ha^{-1})	1750	250	750								1375												
Betula papyrifera																							
Tree density (no. · ha^{-1})		1841	1050	515				19		22		83	128										
Tree basal area ($m^2 \cdot ha^{-1}$)		7.5	24.2	26.0				1.4		1.2		1.0	2.1			211	59						
Tree height (m)		20	16	18						24						0.8	0.3						
Tree diameter (cm)		7.2	17.1	25.4				31.0		26.4		12.3	14.4										
Sapling density (no. · ha^{-1})		102		14				23		12		10	10			6.9	8.7						
Seedling density (no. · ha^{-1})		500	250	1250				625		750			500			26							
Populus balsamifera																							
Tree density (no. · ha^{-1})					1917	675	609	84	28														
Tree basal area ($m^2 \cdot ha^{-1}$)					21.9	32.5	35.5	6.6	1.6														
Tree height (m)					20	30	30																
Tree diameter (cm)					12.1	24.8	27.2	31.8	27.3														
Sapling density (no. · ha^{-1})					8	46		9															
Seedling density (no. · ha^{-1})					500	1750	1250	750															
Picea glauca																							
Tree density (no. · ha^{-1})		249	368	57	49		16	640	538	875	3869	520	64	222									
Tree basal area ($m^2 \cdot ha^{-1}$)		1.6	1.4	0.6	0.2		0.3	47.1	28.7	56.6	27.6	45.9	5.2	1.2	272			78	108				
Tree height (m)								30	21	25	15	26	24	10	3.3			3.3	3.8				
Tree diameter (cm)			7.0	11.4	7.2		14.7	30.6	26.1	28.7	9.5	33.5	32.3	8.4	15								
Sapling density (no. · ha^{-1})		70	102	13	5		374				361			132	12.5			23.1	21.2				
Seedling density (no. · ha^{-1})		8500	2375				2250	500	1500	3500		2125		750									
																		250	250				
Picea mariana																							
Tree density (no. · ha^{-1})													1088	39								3446	4596
Tree basal area ($m^2 \cdot ha^{-1}$)													39.4	0.1	2115	4006	2292	1428	2053	4730	2891	11.5	15.0
Tree height (m)													20	5	35.2	10.2	6.9	23.5	4.6	18.6	6.8	10	7
Tree diameter (cm)													21.5	6.3	15	7	10	13	8	10	8	6.5	6.4
Sapling density (no. · ha^{-1})														29	14.6	5.7	6.2	14.5	5.3	6.5	5.1	88	613
Seedling (layerings) density															10	2052	2024		1721	2783	2772		
(no. · ha^{-1})																						3500	4750
															625	7000	13250	250	16000	25750	27625		
Larix laricina																							
Tree density (no. · ha^{-1})																						203	
Tree basal area ($m^2 \cdot ha^{-1}$)															30							0.4	
Sapling density (no. · ha^{-1})															1.1							27	
Seedling density (no. · ha^{-1})															21.6							2000	
Total																							
Tree density (no. · ha^{-1})	2445	3981	2101	572	1966	675	625	743	566	897	4422	603	1280	261	2417	4217	2351	1506	2161	4730	2891	3649	4596
Tree basal area ($m^2 \cdot ha^{-1}$)	8.7	30.1	33.5	26.6	22.1	32.5	35.8	55.1	30.3	57.8	41.1	46.9	46.7	1.3	39.6	11.0	7.2	26.8	8.4	18.6	6.8	11.9	15.0
Sapling density (no. · ha^{-1})	33	172	115	27	13	420		32		373	361	10	10	161	10	2078	2024		1721	2783	2772	115	613
Seedling density (no. · ha^{-1})	1750	9250	3375	1250	500		3500	1875	1500	4250	1375	2125	500	750	625	7000	13250	500	16250	25750	27625	5500	4750
Stand No.	11	15	16	13	32	25	24	27	26	12	22	31	28	23	30	21	18	19	20	33	34	29	14

[a]Tree names follow Viereck and Little (1972).

TABLE 2. Percent cover of shrubs, herbs, mosses, and lichens in 23 forest stands in interior Alaska. Stands are arranged along an environmental gradient from warm and dry (at left) to cold and wet (at right)[a]

	Quaking aspen		Paper birch		Balsam poplar community			White spruce				White and black spruce			Black spruce								
	Populus tremuloides/ Shepherdia canadensis/ Calamagrostis purpurascens	*Populus tremuloides/ Viburnum edule/ Linnaea borealis*	*Betula papyrifera/ Alnus crispa/ Calamagrostis canadensis*	*Betula papyrifera/ Alnus crispa/ Calamagrostis canadensis*	*Populus balsamifera/ Alnus–Rosa/ Equisetum*	*Populus balsamifera/ Alnus–Rosa/ Equisetum*	*Populus balsamifera/ Alnus–Rosa/ Equisetum*	*Picea glauca/ Rosa acicularis/ Rhytidiadelphus triquetrus*	*Picea glauca/ Rosa acicularis/ Linnaea borealis– Hylocomium splendens*	*Picea glauca/ Hylocomium splendens*	*Picea glauca/ Rosa acicularis– Viburnum edule*	*Picea glauca/ Rosa acicularis– Viburnum edule/ Linnaea borealis– Hylocomium splendens*	*Picea glauca – Picea mariana/ Alnus crispa/ Rhytidiadelphus triquetrus*	*Picea glauca – Picea mariana/ Alnus crispa – Betula glandulosa/ Pleurozium schreberi*	*Picea mariana/ Ledum groenlandicum/ Hylocomium splendens*	*Picea mariana/ Vaccinium vitis-idaea –* feather moss	*Picea mariana/ Vaccinium uliginosum/ Pleurozium schreberi*	*Picea mariana/* feather moss	*Picea mariana/ Ledum groenlandicum/ Pleurozium schreberi*	*Picea mariana/* feather moss	*Picea mariana/* (feather moss– *Cladonia*)– (*Sphagnum*)	*Picea mariana/ Salix/Ledum/ Sphagnum*	*Picea mariana/ Ledum groenlandicum– Sphagnum*
Stand No.	11	15	16	13	32	25	24	27	26	12	22	31	28	23	30	21	18	19	20	33	34	29	14
Tall shrubs																							
Rosa acicularis	15	2	1			24	4	37	4		3	12	13		2		+[b]		+	4	+	2	
Viburnum edule		4	+			1	+		7		5							+				+	
Salix bebbiana			1																				
Alnus tenuifolia					11		26					3											
Salix alaxensis					+																		
Alnus crispa		4	4	22	+	3		10	1	1			6	6	8	+		3		1	+	11	
Rubus idaeus									+														
Salix arbusculoides												+											
Betula glandulosa														34	+								
Salix glauca															+						5		
Salix scouleriana																	2						
Salix planifolia																					+	4	
Low shrubs																							
Shepherdia canadensis	26										+												
Arctostaphylos uva-ursi	7																						
Linnaea borealis		5	1						4	11	+	10	9	1	1								
Vaccinium vitis-idaea			+	3							+	4	4	6	28	16	8	7	12	17	20	42	13
Spiraea beauverdiana													1	1						2	+	1	6
Vaccinium uliginosum		+												16	1	+	11		4	3	4	4	4
Ribes hudsonianum								7					4										
Ledum groenlandicum		+	+											+	11	4	4	2	14	15	21	34	19
Arctostaphylos rubra															1								
Empetrum nigrum														2	3	+	+					1	+
Ledum decumbens														6							3	1	
Vaccinium oxycoccus																						7	1
Herbs																							
Calamagrostis purpurascens	10																						
Pulsatilla patens	3																						
Cnidium cnidifolium	1																						
Erigeron glabellus	+																						
Antennaria rosea	+																						
Poa glauca	+																						1
Equisetum arvense			+								+						+		+				
Corollarhiza trifida		+	+																				
Equisetum pratense						30	2	15	5			1											
Mertensia paniculata						1		3		+	+	+	+										
Lycopodium complanatum			+	2																			
Moeringia lateriflora		1	+						+			+											
Lycopodium annotinum			+													+	+				2		
Pedicularis labradorica			+																				
Solidago multiradiata						1																	
Aconitum delphinifolium								+															
Impatiens noli-tangere								+															
Adoxa moschatellina								+															
Actaea rubra								+															
Gymnocarpium dryopteris								+															
Thalictrum sparsiflorum								+															
Boshniakia rossica													+									32	2
Calamagrostis canadensis		+	+	+		9	3	12		+	+	1	4	2	2	+	+	9	3	5	5		
Galium boreale	4					7		3			+				+								
Epilobium angustifolium	+	+	+			1		+		+	+	+			+								
Pyrola secunda					+				1	+	3	1			4								4
Geocaulon lividum		1	+				+		3	1	1	1			4	3	2	6	+	2	1	+	
Cornus canadensis		+	+					12	+			2	18	1	+	1	+		+		+		
Lycopodium clavatum																+	1						
Pyrola asarifolia								+	1			+			1								
Goodyera repens								+	+				+		+								
Pyrola grandiflora								+					2										
Carex concinna								+															
Carex bigelowii														5								19	
Equisetum sylvatium													32		+		+	7		16	11	13	4
Rubus chamaemorus													+		+				+	2	4		
Equisetum scirpoides		+									+				5								
Saussurrea angustifolium															+							+	
Petasites frigida																				+	1		+
Polygonum alaskanum																							
Mosses																							
Dicranum fuscescens	+	2		+			2			2	1			+	1	2	7		2			+	+
Hypnum spp.	+	2	2	2							4			5									
Hylocomium splendens		2	2	1				12	65	76	7	56	22	2	58	24	7	29	11	56	16	42	15
Rhytidiadelphus triquetrus								45	2			1	51										
Polytrichum spp.		+	+	+				2					+	13		8	7	+	14	9	9	+	3
Brachythecium salebrosum								1							1								
Eurhynchium puchellum								14							+								
Ptilium crista-castrensis		+						1	2				4			1		4		2			
Pleurozium schreberi		+	2	+			+		1	1	7	9		72	2	42	53	56	39	55	77	30	41
Drepanocladus uncinatus			+		1			1	1	+	1	+	1	2	2	2	+		1			+	
Ceratadon purpureus							+													+			
Aulocomnium palustre															2		+		+				
Sphagnum spp.																			+	8	21	29	35
Lichens																							
Cetraria cucullata									+					+						+	3		
Nephroma arcticum		+														5	8				2		3
Cladonia amaurocraea																	+					+	
Cladonia rangiferina														4		1	+		4	3	17	+	3
Cladonia gracilis														+						+	3		
Cladonia sylvaticum		1												+		1	6		1	7	12	+	
Cetraria islandica														1		2	3		2	1	4		+
Peltigera canina		+	+					1	1	2	+	+	1		1	+	2	+	2	4	10	1	
Peltigera aphthosa									1				+	1		2	3		4	2	+	1	
Cladonia fimbriata																					+		
Cladonia alpestris																					+		

[a]Nomenclature is from the following: shrubs (Viereck and Little 1972), herbs (Hultén 1968), mosses (Crum et al. 1965), and lichens (Hale and Culberson 1960).
[b]+, less than 1% cover.

L., and *Pulsatilla patens* (L.) Mill. provide 20% cover. Mosses and lichens are insignificant.

Stand 11: Populus tremuloides/Shepherdia canadensis/Calamagrostis purpurascens

The warmest and driest site conditions are represented by an open aspen stand located on a 75% southeast-facing bluff above the floodplain of the Tanana River at an elevation of 182 m. The adjacent center of the slope is occupied by an *Artemisia*–grassland community. The stand is about 50 years old and it developed after a fire. Trees average 6.7–7 cm in diameter and 10 m in height but the larger trees in the stand are 12 cm dbh and up to 15 m tall. Density of the trees is $2445 \cdot ha^{-1}$ and basal area of the stand is $8.7\ m^2 \cdot ha^{-1}$.

Rosa acicularis is the only tall shrub in the stand, and the low shrub layer is made up primarily of *Shepherdia canadensis* and *Arctostaphylos uva-ursi*. An herbaceous layer has 20% cover and consists of *Calamagrostis purpurascens*, *Galium boreale*, *Pulsatilla patens*, and several herbs characteristic of the adjacent grassland. Mosses and lichens have no significant cover in the stand.

Stand 15: Populus tremuloides/Viburnum edule/Linnaea borealis

The more typical site for aspen is represented by a 60-year-old aspen stand on a 15% south-facing slope along the Chena Hot Springs Road at an elevation of 229 m. Although aspen is dominant, both paper birch and white spruce occur in the stand. Tree density is $3981 \cdot ha^{-1}$ and basal area of the stand is $30.1\ m^2 \cdot ha^{-1}$. Average tree diameters are 11.9 cm, and the average height is 20 m, but the largest aspen in the stand have 20 cm dbh and heights of 23 m. Succession of this stand to white spruce is indicated by the density of white spruce seedlings, $8500 \cdot ha^{-1}$.

Shrubs in the stand are *Viburnum edule, Alnus crispa* (Ait.) Pursh, and *Rosa acicularis* with a total cover of 10% and the subshrub, *Linnaea borealis* L. with 5% cover. Only one herb, *Geocaulon lividum* (Richards.) Fern., has a cover of 1% or more. Mosses and lichens are scattered in the stand and have a total cover of 10% and no single species dominates.

Soils of aspen stands

The two south-facing aspen stands are situated on well-drained silt loams derived from loess that mantles the schist bedrock. Stand 11 occupies an extremely steep, river-cut slope. The Gilmore silt loam (Alfic Cryochrept) tends to be shallow and stony, with bedrock within about 50 cm of the surface. The stonefree, silty surface layer is only about 10 cm thick at this site. Because of high stone content and the steep south-facing slope, this soil is very warm and dry throughout most of the growing season. At best, the site is marginal for growth of aspen.

The soil at stand 15 reflects the effects of a considerably deeper deposit of loess on a more gentle slope. The silt loam soil is essentially free of stones to a depth of about 70 cm, and bedrock is at a depth of at least 1 m. Moisture relations are much more favorable for the growth of trees because of a considerably higher water-holding capacity.

In interior Alaska, aspen is reputed to grow only on warm, well-drained sites. Our observations on the two aspen sites tend to validate that hypothesis. A generalized description of a profile typical of Steese silt loam (Alfic Cryochrept: stand 15) follows: 7–4 cm, recently deposited litter; 4–0 cm, partially decomposed leaf material; 0–3 cm, black (10 YR 2/1)[2] sandy loam, moderate granular structure, friable, roots abundant; 3–9 cm, brown (7.5 YR 4/3) silt loam, moderate angular blocky structure, friable, roots abundant; 9–22 cm, yellowish-brown (10 YR 5/4) silt loam, weak platy structure, friable, roots abundant; 22–25 cm, dark yellowish-brown (10 YR 3/4) silt loam, weak platy structure, friable, roots common; 25–41 cm, olive-brown (2.5 YR 4/4) silt loam, weak platy structure, friable, roots common; 41–80 cm, olive-brown (2.5 YR 4/4) silt loam, moderate platy structure, friable, roots scattered; 80 cm and over, 90% schist fragments.

Closed deciduous forest: paper birch

Two upland birch stands were included in the study. They occur on slightly cooler sites than the aspen stands. Tree density in the stands ranges from $2100 \cdot ha^{-1}$ in a 60-year-old stand to 575 trees $\cdot\ ha^{-1}$ in a 130-year-old stand. Birch tree diameters average 17 cm (dbh) in the young stand and 25.4 cm in the older stand. Total aboveground tree biomass in this forest type ranges from 9192 to 14 713 $g \cdot m^{-2}$, and the annual increment ranges from 343 to 572 $g \cdot m^{-2} \cdot year^{-1}$. Litter fall averages 251 $g \cdot m^{-2} \cdot year^{-1}$.

Both stands have a relatively sparse understory of shrubs, herbs, mosses, and lichens. *Alnus crispa* is the characteristic tall shrub, although its cover is only 4% in the young stand, but 22% in the older stand. Low shrubs are lacking in the old stand, but the subshrubs, *Vaccinium vitis-idaea* L. and *Linnaea borealis*, are present in the younger stand. *Calamagrostis canadensis*, although low in cover, is characteristic of the herbaceous layer. Mosses and lichens are rare, probably because of the heavy leaf litter.

Stand 16: Betula papyrifera/Alnus crispa/Calamagrostis canadensis

[2]Munsell color notation for moist soil.

TABLE 3. Soils information, landform, elevation, slope, and aspect for 21 semi-intensive sites (stands 11–16

Stand No.	Elevation (m)	Slope (%) and aspect	Landform	Soil series	Classification	Parent material
Aspen						
11	182	75 SE	Upper 1/3 slope	Gilmore	Alfic Cryochrept	Loess
15	229	15 S	Lower 1/2 slope	Steese	Alfic Cryochrept	Loess
Birch						
13	381	32 E	Upper 1/3 slope	Gilmore	Alfic Cryochrept	Loess
16	229	15 SSE	Lower 1/3 slope	Fairbanks	Alfic Cryochrept	Loess
Balsam poplar						
24	122	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
25	177	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
32	120	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
White spruce						
12	396	25 S	Upper 1/3 slope	Fairbanks	Alfic Cryochrept	Loess
22	229	18 SE	Upper 1/3 slope	Fairbanks	Alfic Cryochrept	Loess
26	120	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
27	177	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
31	120	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
White spruce/black spruce						
28	177	0	Floodplain	Salchaket	Typic Cryofluvent	Alluvium
23	747	12 S	Upper 1/3 slope	Fairplay	Aquic Cryorthent	Loess and fractured schist
Black spruce						
14	427	30 N	Upper 1/3 slope	Ester	Histic pergelic Cryaquept	Loess
18	468	0	Ridgetop	Fairplay	Aquic Cryorthent	Loess
19	343	2	Midslope saddle	Gilmore	Alfic Cryochrept	Loess
20	167	0	Terrace	Goldstream	Histic pergelic Cryaquept	Alluvium
21	470	15 NW	Ridgetop	Gilmore	Alfic Cryochrept	Loess
29	177	0	Floodplain	Bradway	Pergelic Cryaquept	Alluvium
30	122	0	Floodplain	Bradway	Pergelic Cryaquept	Alluvium
33	400	10 SE	Mid 1/3 slope	Saulich	Histic Pergelic Cryaquept	Loess
34	385	10 SE	Mid 1/3 slope	Saulich	Histic Pergelic Cryaquept	Loess

[a]Measured from organic-mineral interface.

and 18–32) and the Washington Creek intensive site (stands 33 and 34), interior Alaska

Drainage class	Surface texture	Subsoil texture	Forest floor thickness (cm)	Depth to permafrost (cm)	Maximum[a] rooting depth (cm)	Soil degree days
Well drained	Silt loam	Stony loam	2	None	33	2217
Well drained	Loam	Silt loam	8	None	90	1048
Well drained	Silt loam	Stony silt loam	4	None	45	1019
Well drained	Silt loam	Silt loam	4	None	>100	967
Well drained	Fine sandy loam	Fine loamy sand	6	None	>100	1150
Well drained	Fine sandy loam	Silt loam sandy loam	7	None	>90	1310
Well drained	Fine sandy loam	Silt loam loamy sand	5	None	>100	
Well drained	Silt loam	Silty clay loam	9	None	>100	876
Well drained	Silt loam	Silty clay loam	6	None	>100	1117
Well drained	Silt loam	Very fine sandy loam	18	None	>95	798
Well drained	Sandy loam	Silt loam	5	None	85	1140
Well drained	Silt loam	Sandy loam	15	None	>95	
Moderately well drained	Silt loam	Silt loam	25	Occasional deep	50	924
Moderately drained	Stony silt loam	Stony silt loam	10	None	50	676
Poorly drained	Stony silt loam	Stony silt loam	38	22	22	761
Somewhat poorly drained	Silt loam	Stony silt loam	12	None	50	715
Moderately well drained	Silt loam	Silt loam	19	None	48	669
Poorly drained	Silt loam	Silt loam	14	55	55	483
Moderately well drained	Silt loam	Stony silt loam	17	None	50	710
Poorly drained	Silt loam	Silt loam	25	16	16	729
Poorly drained	Silt loam	Silt loam	19	20	20	
Poorly drained	Silt loam	Silt loam	24	51	51	563
Poorly drained	Silt loam	Silt loam	23	35	35	488

This 60-year-old birch stand is located on a 15% south-southeast slope, at an elevation of 229 m, along the Chena Hot Springs Road. The stand has received a number of years of intensive study (Van Cleve and Noonan 1975). Although paper birch is dominant, both aspen and white spruce occur in the stand. Density is 2100 trees $\cdot$ ha^{-1} and the basal area of the stand is 33.5 m^2 $\cdot$ ha^{-1}. The average birch tree diameter is 17.1 cm (dbh) for the dominant birch, and heights average 16 m, the tallest trees being about 23 m. Reproduction is primarily white spruce seedlings, 2375 trees$\cdot$ha^{-1}, with a scattering of aspen and birch seedlings.

The tall shrub layer is scattered and is comprised of *Alnus crispa* and *Rosa acicularis*. Low shrubs and herbs are also low in cover value; *Vaccinium vitis-idaea, Linnaea borealis, Calamagrostis canadensis*, and *Lycopodium annotinum* L. are the most common species. Mosses and lichens are unimportant in the stand.

Stand 13: Betula papyrifera/Alnus crispa/ Calamagrostis canadensis

The 130-year-old paper birch stand is located in Bonanza Creek Experimental Forest at an elevation of 381 m on a 32% east-facing slope. The stand is open, with a density of only 572 trees $\cdot$ ha^{-1} and a canopy cover of about 60%. Basal area of the trees is 26.6 m^2 $\cdot$ ha^{-1}. A few white spruce occur in the stand. Average tree diameter of the birch is 25.4 cm (dbh) and heights average 18 m. Reproduction in the stand is sparse, consisting of a few birch seedlings.

Below the forest canopy is a scattered tall shrub cover of *Alnus crispa* of about 21%. Beneath this the low shrub, herb, moss, and lichen layers are insignificant, having a total cover of only 7%. *Calamagrostis canadensis* and *Lycopodium complanatum* L. are the most common herbs.

Soils of paper birch stands

Both birch stands are located on upland slopes with well-drained silt loam soils. The soil at stand 13 is a Gilmore silt loam (Alfic Cryochrept), with shallow stony horizons and bedrock within 1 m of the surface. The soil at stand 16, on the other hand, is deep and stone-free with no hint of approaching bedrock at depths greater than 1 m. This soil is classified as Fairbanks silt loam (Alfic Cryochrept); the soil is described in the white spruce section. Birch may also develop on soils with a shallow active layer.

Forest floor layers are thin and consist mainly of birch leaves in varying stages of decay. Moss is almost completely absent from these forest floors; as a result, organic materials do not accumulate nearly as fast.

A generalized description of a profile typical of Gilmore silt loam (stand 13) follows: 4–3 cm, recently deposited litter, mainly birch leaves; 3–0 cm, very dark brown humus; 0–6 cm, dark brown (7.5 YR 4/4) silt loam, weak subangular blocky structure, friable, roots common; 6–19 cm, light olive-brown (2.5 YR 5/4) silt loam, weak platy structure, friable, roots common; 19–38 cm, light yellowish-brown (2.5 YR 6/4) with small yellowish-brown (10 YR 5/6) mottles stony silt loam, weak platy structure, friable, 35% schist gravels and cobbles, roots scattered; 38–57 cm and over, olive-brown (2.5 YR 4/4) stony sandy loam, single grained (structureless), 50% angular schist fragments, roots absent.

Closed broadleaf forest: balsam poplar

Three balsam poplar stands were studied: one on the floodplain of the Chena River and two on the floodplain of the Tanana River. All three have become established on newly exposed river alluvium and are part of the floodplain successional series from willow–alder thickets to balsam poplar to white spruce and eventually to black spruce (Viereck 1970). These balsam poplar stands, abundant on the floodplains in the region, are the most productive forest stands. Aboveground tree biomass ranged from 4100 to 18 000 g$\cdot$m^{-2}. Annual tree production averages 551 g $\cdot$ m^{-2} $\cdot$ year^{-1} but may reach 952 g $\cdot$ m^{-2} $\cdot$ year^{-1} on the most productive sites. Litter fall averages 390 g $\cdot$ m^{-2} $\cdot$ year^{-1}.

Environmentally these stands compare with the upland aspen and birch stands with accumulated soil degree day sums averaging between 900 and 1300, but the plant species are different (Table 2). The forest floor layer consists of about 2 cm of leaf litter, litter fall being between 268 and 653 g $\cdot$ m^{-2} $\cdot$ year^{-1}. Mosses are limited to about 1% cover, primarily around the bases of the tree stems. Low shrubs, which comprise an important component of upland black spruce stands, are entirely lacking in the balsam poplar stands.

Stand 32: Populus balsamifera/Alnus–Rosa/ Equisetum

The 50-year-old balsam poplar stand on the Tanana River floodplain is considerably less productive than the same aged stand in the Chena River. The density of the balsam poplar is 1917 trees $\cdot$ ha^{-1}, average diameters (dbh) are only 12.1 cm, and heights are about 20 m. Basal area of the trees is 22.1 m^2 $\cdot$ ha^{-1}. In spite of the higher tree density, the canopy is open, only 50% cover.

The tall shrub layer is variable within this stand but averages about 30%. It is composed of decadent clumps of *Alnus tenuifolia* and *Salix alaxensis* (Anderss.) Cov. which reach heights of 10 to 15 m and have only recently been overtopped by the trees. A number of balsam poplar seedlings or root suckers are developing in the areas that have opened up as the result of the breaking up of the tall shrub canopy. The herb layer is

TABLE 4. Aboveground tree biomass and annual production and vascular plant litter fall for the principal forest types in interior Alaska (grams per square metre)

Forest type	Number of stands	Tree biomass		Annual tree production		Litter fall	
		Range	$x \pm$ SE	Range	$x \pm$ SE	Range	$x \pm$ SE
Black spruce	4	1586–10984	5094±2107	57–148	109±20	15–142	43±11
White spruce	4	6152–24577	17442±4279	238–540	366±63	95–316	155±78
Quaking aspen	2	4653–17490	11071±6419	363–760	567±199	27–222	156±65
Paper birch	3	9192–14713	11156±1782	343–572	470±67	233–265	251±8
Balsam poplar	3	4067–18027	12097±4165	264–952	552±206	268–653	389±49

composed almost entirely of *Equisetum pratense* which has a cover value of 29%; all other herbs have less than 0.5% cover. Mosses are unable to tolerate the heavy litter fall and are found at the base of the trees, making up about 1% cover.

Stand 25: Populus balsamifera/Alnus–Rosa/Equisetum

This 60-year-old balsam poplar stand on the floodplain of the Chena River at an elevation of 177 m is the most productive of all interior forest stands that we have measured. The dominant balsam poplar trees are 25 to 30 m tall and average 24.8 cm in diameter (dbh). Tree density is 675 trees $\cdot$ ha^{-1}, and the tree canopy cover is about 90%. Basal area is 32.5 m^2 $\cdot$ ha^{-1} and the mean annual increment is 952 g $\cdot$ m^{-2}.

Alnus crispa is scattered in the stand, and there is a well-developed shrub layer of *Rosa acicularis* with a scattering of *Viburnum edule*. Horsetails, primarily *Equisetum pratense* L. and *E. arvense* L., are predominant in the herbaceous layer and, together with *Calamagrostis canadensis* and *Galium boreale*, make up most of the 43% herb cover. A few mosses occur at the bases of the poplar trees where they are slightly above the heavy leaf litter. Reproduction in the stand consists of some saplings of balsam poplar that may have developed as root shoots and a number of white spruce seedlings and saplings with a density of 150 $\cdot$ ha^{-1}.

Stand 24: Populus balsamifera/Alnus–Rosa/Equisetum

The 100-year-old balsam poplar stand 20 km southwest of Fairbanks on the Tanana River floodplain at an elevation of 122 m is in the process of breaking up and represents an older stage of balsam poplar development on the floodplain. There is considerable rot in the base of the tree stems, and several large trees have fallen in the past few years. The dominant trees are 30 m in height and average 27.2 cm in diameter (dbh). Tree density is low, 609 trees $\cdot$ ha^{-1}, and the tree canopy rather open, about 40% cover. Basal area of the trees is 36 m^2 $\cdot$ ha^{-1}. There are a few scattered white spruce in the stand but with a density of only 16 $\cdot$ ha^{-1}. Seedling reproduction is balsam poplar, 1250 $\cdot$ ha^{-1}, and white spruce, 2250 $\cdot$ ha^{-1}.

The tall shrub layer in this stand has about 40% cover and is primarily *Alnus tenuifolia* Nutt. with only a small amount (4%) of *Rosa acicularis* and *Viburnum edule*. The herb layer is sparse (total cover 2%) and is primarily *Equisetum pratense*. As with the other balsam poplar stands, there is no significant moss cover.

Soils of balsam poplar stands

The three balsam poplar stands are located on the level floodplain immediately adjacent to the Tanana River (stands 24 and 32) or Chena River (stand 25). Soil parent materials are dominantly sandy alluvium, although localized lenses of silty sediments are also present. Soils are deep and well drained and so immature that effects of soil-forming processes are not very noticeable. Instead, the soil profile features are mainly a result of the depositional history of the alluvium. An unusual feature of these soils is the presence of a number of buried forest floor layers, in various stages of decomposition. Each of these layers represents a surface that was exposed for a number of years before it too was buried by a fresh covering of alluvial sediments. These soils are underlain by gravel at a depth of over 1 m.

All six profiles examined are classified in the Salchaket soil series (Typic Cryofluvent). The principal difference among profiles is fewer buried organic layers in the soil as in stand 25, where there is only one shallow layer, probably buried by deposition of the flood of 1967.

A generalized profile description taken at stand 24 (mature balsam poplar along the Tanana River) follows: 0–8 cm, grayish-brown (10 YR 5/2) fine sandy loam, weak platy structure, very friable, roots plentiful; 8–10 cm, brown forest floor material, leaf parts distinguishable, very abundant roots; 10–13 cm, grayish-brown (10 YR 5/2) and dark yellowish-brown (10 YR 4/6) loam, weak angular blocky structure, friable, roots plentiful; 13–14 cm, dark brown, well-decomposed organic material, very abundant roots; 14–22 cm, dark grayish-brown (2.5 YR 4/2) with brown (7.5 YR 4/4) mottles fine loamy sand, weak subangular blocky structure, very friable, roots plentiful; 22–25 cm, brown distinguishable leaf remains interbedded with thin

sediment lenses; 25–35 cm, dark grayish-brown (2.5 YR 4/2) with brown (7.5 YR 4/4) mottles silt loam, weak angular blocky structure, friable, roots common; 35–36 cm, dark brown, well-decomposed organic material; 36–40 cm, grayish-brown (2.5 YR 5/2) with brown (7.5 YR 4/4) mottles silt loam, weak angular blocky structure, friable, roots common; 40–41 cm, dark brown, well-decomposed organic material; 41–65 cm, dark grayish-brown (10 YR 4/2) with abundant yellowish-brown (10 YR 5/6) mottles fine sandy loam, massive, friable, roots scattered; 65–105 cm, dark grayish-brown (2.5 YR 4/2) fine loamy sand, massive, very friable, roots scattered; 105 cm and over, water-worn gravels.

Closed conifer: white spruce

Five white spruce stands were included in our study. Three are mature stands on the floodplains of the Chena (27) and Tanana rivers (26, 31), and two are on south-facing upland slopes. Two ages are represented in the upland stands: a 70-year-old stand that apparently came in directly after a fire (22) and a 165-year-old stand of large mature trees (12). These white spruce stands represent the commercial forest sites in interior Alaska. They usually occur on warm permafrostfree sites adjacent to rivers and on south-facing slopes with deep loess parent material.

Tree density may be high in young successional stands on these sites but is low in the older stands, 550–750 trees $\cdot$ ha^{-1}. In the mature stands tree size averages about 30 cm in diameter and 25–35 m in height. Basal area ranges from 30 to 60 m$^2 \cdot$ ha^{-1} and aboveground tree biomass of mature stands from 24 000 to 26 000 g $\cdot$ m^{-2}. Annual productivity may reach 540 $\cdot$ m$^{-2} \cdot$ year^{-1}, and litter fall averages 155 g $\cdot$ m$^{-2} \cdot$ year^{-1}.

Rosa acicularis is the most conspicuous tall shrub in these white spruce stands but scattered clumps of *Alnus crispa* and some *Viburnum edule* are also typical. Low shrubs and herbs may be sparse to abundant, depending on overstory density, and consist primarily of *Linnaea borealis*, *Equisetum* spp., *Geocaulon lividum*, and *Pyrola* spp. The forest floor has a nearly continuous moss mat of *Hylocomium splendens* (Hedw.) B.S.G. which in some floodplain stands may also contain a high cover of *Rhytidiadelphus triquetrus* (Hedw.) Warnst. Lichens make up a small component of the forest floor.

Stand 27: Picea glauca/Rosa acicularis/Rhytidiadelphus triquetrus

This 130-year-old white spruce stand on the floodplain of the Chena River at an elevation of 177 m has developed from a successional stage in which balsam poplar was more abundant. Old decaying balsam poplar are standing among the spruce, and fallen balsam poplar are common on the forest floor. The density of spruce trees is 640 trees $\cdot$ ha^{-1}, their average diameter is 30.6 cm, and the height of the dominants is 27 to 30 m. Basal area of the trees is 55 m$^2 \cdot$ ha^{-1}. Reproduction of spruce, birch, and balsam poplar is scattered in the stand.

Beneath the forest canopy are scattered clumps of *Alnus crispa* and an abundant layer of *Rosa acicularis*. The herbaceous layer is well developed, with an overall cover of 48%. It is dominated by *Equisetum pratense*, *Calamagrostis canadensis*, *Galium boreale*, and *Cornus canadensis*. The most important species in the nearly continuous moss layer is *Rhytidiadelphus triquetrus*, a common moss in floodplain white spruce stands. The exceptionally rich herbaceous layer in this stand may be the result of frequent flooding which adds nutrient to the forest floor and tends to reduce the moss cover.

Stand 26: Picea glauca/Rosa acicularis/Linnaea borealis – Hylocomium splendens

This white spruce stand on the floodplain of the Tanana River is located on Sam Charley Island, at an elevation of 120 m. In addition to the 115-year-old white spruce, there are occasional decadent balsam poplar in the stand. Diameters of the dominant spruce trees average 30 cm, and their heights are 25 to 27 m. Tree density is low, 566 trees $\cdot$ ha^{-1}, and the basal area is 30.4 m$^2 \cdot$ ha^{-1}. Seedlings of white spruce are scattered throughout the stand and have a density of 2500 $\cdot$ ha^{-1}.

The tall shrub layer is dominated by *Rosa acicularis*, with an occasional clump of *Alnus crispa*. The low shrub and herb layers together cover 20% and are composed primarily of *Linnaea borealis*, *Equisetum pratense*, *Geocaulon lividum*, *Pyrola secunda* L., and *Pyrola asarifolia* Michx. *Hylocomium splendens* provides most of the moss cover, and lichens are unimportant in the stand.

Stand 12: Picea glauca/Hylocomium splendens

This 165-year-old, upland white spruce stand, typical of commercial forest stands in interior Alaska, is located at an elevation of 396 m on a 25% south-facing slope in Bonanza Creek Experimental Forest. Diameters of dominant trees range from 35 to 43 cm and average 29 cm, heights range from 30 to 36 m and average 25 m. Canopy cover is about 60%, tree density is 897 trees $\cdot$ ha^{-1}, and the basal area is 58 m$^2 \cdot$ ha^{-1}. Occasional paper birch and aspen persist beneath the spruce canopy. Reproduction of white spruce seedlings is abundant in the stand, density 3500 $\cdot$ ha^{-1}.

Shrubs are scarce; scattered *Alnus crispa* and *Viburnum edule* make up less than 1% cover. Herbaceous cover is also low and consists of *Calamagrostis canadensis*, *Geocaulon lividum*, and *Pyrola secunda*. The forest floor is covered by a moss mat made up

almost entirely of *Hylocomium splendens*. *Peltigera canina* (L.) Willd. is the main foliose lichen species.

Stand 22: Picea glauca/Rosa acicularis – Viburnum edule

This dense stand of relatively young, white spruce is located in a south-southeast facing slope of about 20% on a ridge about 40 km southwest of Fairbanks. Apparently the stand came in after a fire about 70 years ago as a mixed aspen and spruce stand. It was selected as representative of a young stage of white spruce stand development. White spruce has a density of 3870 trees $\cdot$ ha^{-1} and the density of aspen is 550 trees $\cdot$ ha^{-1}. The tree canopy cover is nearly 80%. The average diameter of the spruce is 9.5 cm, and the height of dominant trees is 15 to 20 m. Total aboveground tree biomass is high, 25 000 g $\cdot$ m^{-2}, and aboveground tree production is 81 g $\cdot$ m^{-2}. Reproduction consists of 1375 aspen suckers $\cdot$ ha^{-1}.

In spite of this dense canopy, a shrub layer of *Rosa acicularis* and *Viburnum edule* makes up about 8% cover, but the cover of low shrubs and herbs is only 2% for each group. Surprisingly for a spruce stand in this area, the moss layer of *Hylocomium splendens* has only 14% cover.

Stand 31: Picea glauca/Rosa acicularis – Viburnum edule/Linnaea borealis – Hylocomium splendens

The oldest white spruce stand we studied is a 250-year-old stand on the floodplain of the Tanana River at an elevation of 120 m. In addition to the white spruce, there are occasional paper birch. The density of spruce is low, 520 $\cdot$ ha^{-1}, but average tree diameters are large (33.5 cm); the largest diameter in the stand is 50 cm. The stand is beginning to break up; several large trees have fallen in the past decade. White spruce seedlings have a density of 2125 $\cdot$ ha^{-1}, but none have reached a metre in height in spite of the new openings and increased light in the stand.

The tall shrub layer consists of 10% cover of *Rosa acicularis* and occasional clumps of *Alnus tenuifolia*. The low shrub and herb layer is not well developed, and only *Linnaea borealis, Vaccinium vitis-idaea*, and *Cornus canadensis* L. have more than 1% cover. The dominant moss is *Hylocomium splendens*, but *Pleurozium schreberi* (Brid.) Mitt. has a 9% cover value. *Peltigera canina*, the only lichen in the forest floor, has less than 1% cover.

Soils of white spruce stands

The soils supporting all five white spruce stands are deep, well drained, and permafrost-free. Three stands (26, 27, and 31) are situated on river floodplains and have Salchaket soils (Typic Cryofluvents) similar to those supporting the balsam poplar stands. These are deep soils, developing in stratified alluvial sediments, and underlain at considerable depth by water-worn gravels. The soil at stand 26 has a surface silt loam horizon, and the subsoil ranges from sandy loam to very fine sand in texture. The surface soil at stand 27 is a sandy loam; in addition to sand and gravel, the subsoil has two layers of silt loam.

The upland stands (12 and 22) have soils classified as Fairbanks silt loam (Alfic Cryochrept). These soils are developing in deep deposits of aerially deposited loess. The degree of profile development is not great, although a textural and darker B-horizon is sometimes present. Reflecting the parent material, soil texture is most often silt loam in all horizons, which are, in general, remarkably stonefree. Thickness of the forest floor averages only about 7 cm, despite the fact that moss cover was virtually complete in these stands.

Soils supporting white spruce are among the warmest and most well-drained soils in the area. A generalized description of a profile typical of Fairbanks silt loam (stand 22) follows: 8–5 cm, live moss and recently deposited litter; 5–0 cm, dark brown mat of coarse fibrous moss remains and forest litter, roots abundant; 0–4 cm, dark brown (10 YR 3/3) silt loam, weak granular structure, friable, roots abundant; 4–10 cm, brown (10 YR 4/3) silt loam, moderate subangular blocky structure, friable, roots abundant; 10–25 cm, brown (10 YR 4/3) silt loam, weak subangular blocky structure, friable, roots common; 25–30 cm, dark yellowish-brown (10 YR 3/4) silty clay loam, weak platy structure, firm, roots common; 30–39 cm, brown (10 YR 4/3) silt loam, weak platy structure, slightly firm, roots common; 39–100 cm and over, dark grayish-brown (2.5 YR 4/2) silt loam, weak platy structure, friable, roots common, decreasing with depth.

Closed conifer: mixed white and black spruce

Stand 28: Picea glauca – P. mariana/Alnus crispa/ Rhytidiadelphus triquetrus

The mixed white spruce and black spruce stand on the floodplain of the Chena River represents a transition from the productive floodplain white spruce stands to the less productive black spruce stands on the older terraces. This stand was earlier described by Viereck (1970). The dominant trees are 200-year-old white spruce with an average dbh of 27.7 cm and an average height of 24 m. Between the older trees are 140-year-old white and black spruce and an occasional paper birch. Total tree density is 1450 trees $\cdot$ ha^{-1} and the basal area of the stand is 46.7 m^2 $\cdot$ ha^{-1}. Reproduction in the stand is limited to a few birch seedlings, 500 $\cdot$ ha^{-1}.

Scattered *Alnus crispa, Rosa acicularis*, and *Viburnum edule* form a shrub layer with about 20% cover. Low shrubs and herbs are abundant in the stand;

Equisetum sylvaticum L., *Cornus canadensis*, *Vaccinium vitis-idaea*, and *Calamagrostis canadensis* are most common. The moss layer is dominated by *Rhytidiadelphus triquetrus* and *Hylocomium splendens*.

Conifer woodland: mixed white and black spruce

Stand 23: Picea glauca – P. mariana/Alnus crispa – Betula glandulosa/Pleurozium schreberi

The coldest site in our study is represented by an open mixed white and black spruce stand at treeline at 747-m elevation on Wickersham Dome. This site is at the upper limit of large mature spruce, but younger spruce about 40 years old are common well above the older established treeline (Viereck 1979). The stand is very open, with a tree density of 262 trees · ha^{-1} and a canopy cover of 8%. Most of the trees are white spruce, but there are some black spruce, about 40 · ha^{-1} in the stand. Tree diameters (dbh) average 8.4 cm and heights average 5 m, but some of the larger white spruce are up to 21.5 cm dbh and 10 m in height. Basal area of the stand is only 1.3 $m^2 \cdot ha^{-1}$. Tree ages range from 110 to about 150 years. Reproduction consists of scattered spruce seedlings and saplings, most of which are about 40 years old.

Betula glandulosa and *Alnus crispa* form dense thickets in the stand and have a total cover of 40%. Low shrubs are abundant between the tall shrub clumps and consist mainly of *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Ledum decumbens*, and *Empetrum nigrum*. The herb layer is sparse and comprises *Carex bigelowii* and *Calamagrostis canadensis*. The moss cover is nearly continuous and is made up mostly of *Pleurozium schreberi* and *Polytrichum* spp. *Cladonia rangiferina* is the most important lichen species, with a cover of about 4%.

Closed conifer, open conifer, and conifer woodland: black spruce

Nine stands in which black spruce is dominant are included in this series. All are relatively unproductive stands in which tree growth is slow but moss productivity high. The stands vary from those with tree canopy cover of 60% or more to woodland stands with less than 25% canopy cover. Heights and diameters of the dominant trees range from 18 m and 15 cm, respectively, on the better sites, to 5 m and 5.6 cm, respectively, on the poorer permafrost-dominated site. Tree densities range from 1428 to 4730 trees · ha^{-1}. Tree biomass ranges from 148 to 1586 $g \cdot m^{-2}$. Litter fall averages 43 $g \cdot m^{-2} \cdot year^{-1}$, but ranges from 15 to 142 $g \cdot m^{-2} \cdot year^{-1}$.

All of the stands are characterized by a sparse layer of tall shrubs mostly of isolated clumps of *Alnus crispa* and a well-developed layer of low shrubs, mostly *Vaccinium uliginosum* L., *Ledum groenlandicum* Oeder., and *Vaccinium vitis-idaea*. The most characteristic feature of all the stands is a thick, lush moss mat of the two feathermosses, *Hylocomium splendens* and *Pleurozium schreberi*, but with as much as 34% cover of *Sphagnum* spp. on the coldest and wettest sites. Fruticose lichens, primarily *Cladonia* spp., are most abundant in the open sites, and foliose lichens, especially *Peltigera* spp. and *Nephroma arcticum* (L.) Willd. occur commonly in the closed stands. However, in some black spruce stands lichen cover may be as low as 1%.

Stand 30: Picea mariana/Ledum groenlandicum/ Hylocomium splendens

This stand is located on an older terrace of the active floodplain of the Tanana River at an elevation of 122 m. Black spruce is the dominant tree, but there are scattered white spruce and tamarack in the stand, with a total canopy cover of 60%. It was chosen to represent a late stage of floodplain succession. The total tree density is 2400 · ha^{-1}, and the basal area is 40 $m^2 \cdot ha^{-1}$. The oldest trees in the stand are 140 years old, and the average age is about 120 years. The average diameter of the dominant trees is 14.6 cm, and their height is about 15 m.

Tall shrubs, primarily *Alnus crispa* and *Rosa acicularis*, have about 10% cover. Low shrubs form a nearly continuous cover, with *Vaccinium vitis-idaea*, *Ledum groenlandicum*, and *Empetrum nigrum* L. the most common. Herbs are not important on the stand; 15 species have total cover of 13%, and only *Equisetum scirpoides*, *Geocaulon lividum*, and *Calamagrostis canadensis* have cover values of more than 1%. The moss layer is thick and continuous and consists almost totally of *Hylocomium splendens*. Depressions that remain filled with water most or all of the summer are common, and the active layer is shallow, only 20 cm of the mineral soil thaws.

Stand 21: Picea mariana/Vaccinium vitis-idaea/ *feather moss*

This stand is near a ridgetop on a north-facing slope of about 15% at the highest elevation in Bonanza Creek Experimental Forest, 470 m. This stand has received considerable study in the past (Barney and Van Cleve 1973; Barney et al. 1978; Van Cleve et al. 1981). The trees in the stand are about 60 years old. Tree density is 4200 trees · ha^{-1} and includes about 200 paper birch · ha^{-1}; total tree canopy is about 50%. Tree diameters average 5.7 cm and heights average about 7 m, with dominant trees reaching 12 cm in diameter and 9 m in height. The basal area is 11 $m^2 \cdot ha^{-1}$.

Tall shrubs are lacking in this stand. Low shrubs have 22% cover and consist primarily of *Vaccinium vitis-idaea*, *Ledum groenlandicum*, and *Vaccinium uliginosum*. Herbs are scarce, and only *Geocaulon lividum* has more than 1% cover. *Pleurozium schreberi*, *Hylocomium splendens*, and *Polytrichum* spp. cover 76% of the forest floor. A number of lichens make up 13% cover but only *Nephroma arcticum*, *Peltigera*

aphthosa (L.) Willd., and *Cetraria islandica* (L.) Ach. have more than 1% cover.

Stand 18: Picea mariana/Vaccinium uliginosum/ Pleurozium schreberi

The black spruce stand adjacent to the Wickersham fire area on a level site at an elevation of 468 m was used as a control for the Wickersham study, and the description is derived from Viereck and Dyrness (1979). The stand consists of a scattering of older trees that survived a fire about 75 years ago and a predominance of trees about 75 years old. The height of the older trees averages 15 m, but the younger trees have an average height of 8 to 10 m. Diameters of the larger trees are 12 to 15 cm, and the average diameter of the younger trees is 7.5 cm. The tree density is 2300 trees $\cdot$ ha^{-1}, and the basal area is 6.9 m^2 $\cdot$ ha^{-1}. Black spruce regeneration is dense, 13 000 stems $\cdot$ ha^{-1}, primarily as the result of layering.

Tall shrubs in the stand consist of scattered decadent clumps of *Salix scouleriana* Barratt. Low shrubs have a cover of 23% and consist primarily of *Vaccinium uliginosum*, *V. vitis-idaea*, and *Ledum groenlandicum*. The herbaceous layer is sparse but mosses, predominantly *Pleurozium schreberi*, have 70% cover. Lichens, both foliose and fruticose species, have a cover of 32% and are dominated by *Nephroma arcticum*, *Cladonia rangiferina*, and *Peltigera aphthosa*.

Stand 19: Picea mariana/*feather moss*

This black spruce stand in the middle of a generally south-facing slope lies along the crest of a rounded ridge that slopes slightly to the north and east. It is the most productive of the black spruce sites sampled in interior Alaska. The average age of trees in the stand is 130 years; the oldest sample is 165 years. The average diameter is 14.5 cm, and the average height is 13 m. A few dominants reach 17 m in height and 34 cm in diameter. The tree density, primarily black spruce, is 1565 trees $\cdot$ ha^{-1} and the basal area is 27.1 m^2 $\cdot$ ha^{-1}. In addition to the black spruce, there are occasional paper birch and white spruce in the stand, but neither species has significant cover. There is almost no reproduction in the stand.

The tall shrub layer of *Alnus crispa* is sporadic and makes up only 37% cover. Low shrubs are also sparse, with *Vaccinium vitis-idaea* and *Ledum groenlandicum* making up 9% cover. An herb layer of about 22% comprises mostly *Calamagrostis canadensis*, *Equisetum sylvaticum*, and *Geocaulon lividum*. The moss layer of *Hylocomium splendens* and *Pleurozium schreberi* is lush and covers about 90% of the stand. Lichens make up only 3% of the forest floor cover.

Stand 20: Picea mariana/Ledum groenlandicum/ Pleurozium schreberi

This black spruce stand is located on an old terrace of the Tanana River well above the flood level at an elevation of 183 m and was studied in detail by Barney and Van Cleve (1973). The stand has two ages of trees which have probably resulted from a fire that did not completely kill the original stand. The older trees are about 100 years old and the younger trees average 57 years. Dominant heights are 8 m, but the younger trees average about 4.4 m. A few larger white spruce are also scattered in the stand. The basal area of the spruce is 8.4 m^2 $\cdot$ ha^{-1}. Reproduction is abundant, primarily from layering of black spruce.

The shrub layer consists of scattered *Rosa acicularis* and an abundance of *Vaccinium vitis-idaea*, *Ledum groenlandicum*, and *Vaccinium uliginosum*. A herbaceous layer of 5% cover is made up primarily of *Calamagrostis canadensis*. A moss cover of 68% is dominated by *Pleurozium schreberi*, with lesser amounts of *Polytrichum* spp. and *Hylocomium splendens*. Although on a lowland site with cold, wet soils, *Sphagnum* spp. makes up less than 1% cover. Lichens, mainly *Peltigera aphthosa*, *Cladonia rangiferina*, *Cladonia* spp., and *Cetraria islandica* have a cover value of 18%.

Intensive site: Washington Creek: stands 33 and 34

The site selected for the intensive study of the black spruce ecosystem is a gently sloping 10%, southeast-facing hillside in the Washington Creek Fire Ecology Research Area, about 45 km north of Fairbanks. The site is represented by two black spruce communities, a closed black spruce − feather-moss type in the upper half and an open black spruce (feather moss−*Cladonia*)−(*Sphagnum*) transition in the lower half. The description of the site follows that of Dyrness and Grigal (1979).

Stand 33: upper stand (400 m elevation): Picea mariana/*feather moss*—The overstory black spruce on this site are about 140 years old and have an average diameter of 6.5 cm, a height of 8−10 m, and a basal area of 18.6 m^2 $\cdot$ ha^{-1}. Density of trees and saplings is high, 7500 stems $\cdot$ ha^{-1}. Black spruce regeneration is abundant, over 25 000 $\cdot$ ha^{-1} mainly because of layering of basal branches. The shrub layer is scattered and is made up primarily of low shrubs, such as *Ledum groenlandicum*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea*. Tall shrubs, primarily *Alnus crispa*, make up about 5% cover and occur only sporadically. The herb layer is also poorly developed, with *Equisetum sylvaticum* and *Calamagrostis canadensis* the most important species. The moss layer, on the other hand, is luxuriant; the entire forest floor is covered by a thick layer dominated by *Pleurozium schreberi*, *Hylocomium splendens*, and *Polytrichum juniperinum*. Lichens, primarily several species of *Cladonia*, but also species of *Peltigera* and *Nephroma arcticum*, make up about 35% cover.

Stand 34: lower stand (385 m elevation): Picea mariana – (*feather moss*–Cladonia)–(Sphagnum)— The lower part of the intensive site was described by Dyrness and Grigal (1979) as an open black spruce – (feather moss – *Cladonia*)–(*Sphagnum*) intergrade, with *Sphagnum* spp. in the lower areas and *Cladonia* spp. dominating the slight rises. The overstory black spruce is open and density of trees is 2900 trees $\cdot$ ha^{-1}. The average diameter is 5.1 cm, and the height is only 6–8 m. Basal area of trees is 6.8 m^2 $\cdot$ ha^{-1}. The average age of the trees is about 120 years, but trees as old as 150 years occur in the stand. The principal shrubs, which have about 60% cover, are *Ledum groenlandicum, Vaccinium uliginosum, Betula glandulosa*, and *Vaccinium vitis-idaea*. Herbs, which make up 25–30% cover, include *Calamagrostis canadensis, Rubus chamaemorus* L., and *Equisetum sylvaticum*. *Sphagnum* and feather moss–*Cladonia* patches occur as a mosaic with *Sphagnum* dominating the depressions and *Cladonia* lichens and feather mosses the elevated areas.

Stand 29: Picea mariana/Salix–Ledum/Sphagnum

This open black spruce stand is located on an older terrace of the Chena River at an elevation of 177 m. The stand was used as part of a successional study and has been described by Viereck (1970). It consists of black spruce and an occasional tamarack (*Larix laricina* (DuPoi) K. Koch). The average age of the spruce is about 130 years, their average height is 10 m, and their average dbh is 6.5 cm. The density of the trees is 3820 trees $\cdot$ ha^{-1} and the canopy cover is 30%. Aboveground tree production is low at about 15 g $\cdot$ m^{-2} $\cdot$ year^{-1}. Reproduction is primarily by layering of the black spruce and by seedlings of the tamarack.

A few scattered clumps of *Salix planifolia* spp. *pulchra* (Cham.) Argus, *Salix alaxensis*, and *Alnus crispa* occur in openings between the spruce. Low shrubs, *Ledum groenlandicum, Ledum decumbens*, and *Vaccinium uliginosum*, form a nearly continuous layer with a total cover of 90%. Herbs are also abundant, 66% cover, and consist mainly of *Calamagrostis canadensis, Equisetum sylvaticum*, and *Rubus chamaemorus*. Mosses are abundant and dominated by *Sphagnum squarrosum* (Sw. ex. Croms) and *S. warnstorfianum* Du Rietz along with *Hylocomium splendens* and *Pleurozium schreberi*.

Stand 14: Picea mariana – Ledum groenlandicum – Sphagnum

Stand 14 is on a 30% north-facing slope at an elevation of 427 m in Bonanza Creek Experimental Forest and was selected to represent the cold, wet, low productivity, upland sites. This stand was contrasted with an adjacent south-facing white spruce stand (stand 12) in an earlier study (Krause et al. 1959). Older trees in the stand are about 145 years old, and the average age is 125 years. The black spruce are very slow growing; the average height of the dominants is 7.0 m and their average diameter is 6.4 cm. Although the density of trees in the stand is relatively high, 4600 trees $\cdot$ ha^{-1}, because they are small and narrow crowned the total tree cover is only 12%. The basal area of the trees is 15 m^2 $\cdot$ ha^{-1}. Regeneration of black spruce in the form of layering from lower branches is abundant.

The tall shrub layer in this stand consists of a few isolated clumps of *Alnus crispa*. Low shrubs are abundant; the 43% cover is composed primarily of *Ledum groenlandicum, Vaccinium vitis-idaea, Vaccinium uliginosum*, and *Spiraea beauverdiana*. The herbaceous layer is sparse; *Rubus chamaemorus* and *Geocaulon lividum* are most abundant. In spite of the steepness of the slope, *Sphagnum* spp. are abundant, 35% cover, and with *Pleurozium schreberi* and *Hylocomium splendens*, mosses make up a total cover of 94%. *Nephroma arcticum* and *Cladonia rangiferina* are the most abundant lichens.

Soils of black spruce stands

Black spruce stands are situated on six different soil series in both floodplain and upland positions (Table 3). Six of the nine black spruce stands have soils exhibiting a shallow permafrost layer. Soils lacking permafrost (stands 18, 19, and 21) are shallow to schist bedrock. One soil characteristic that all the black spruce stands share is a mineral surface horizon of silt loam texture. The silty parent material in the two stands adjacent to the river (29 and 30) is alluvial material; in the upland stands, it is loessial in origin. With the exception of the Gilmore silt loam soils (Alfic Cryochrepts, stands 19 and 21), which are moderately well drained, all soils supporting the black spruce stands are poorly drained. The soil profiles examined are generally immature, with little development of horizons beyond an A horizon. Forest floors, on the other hand, are consistently well developed, averaging about 23 cm in thickness. These forest floor layers, made up mainly of moss remains, decompose slowly and thus build up rapidly as stand age increases.

The soils supporting black spruce are the wettest and coldest of all soils supporting tree growth. Although these conditions may generally be attributed to very thick forest floors and the consequent appearance of shallow permafrost, they also exist in certain soils on upper slopes and ridgetops that lack permafrost.

A general profile description from stand 33 in the intensive study site (Saulich silt loam; Histic Pergelic Cryaquept) follows: 25–18 cm, live moss and recently deposited litter; 18–5 cm, dark reddish-brown (5 YR 3/2) mat of coarse fibrous moss remains and forest litter, roots abundant; 5–0 cm, black (5 YR 2.5/1) humus, roots abundant; 0–7 cm, very dark grayish-brown (10 YR 3/2) silt loam, weak subangular blocky structure, friable, roots common; 7–25 cm, dark

grayish-brown (2.5 YR 4/2) saturated silt loam, many indistinct dark yellowish-brown (10 YR 4/4) mottles, massive, sticky and plastic, roots scattered; 25 cm and over, permafrost.

Discussion

Environmental gradient

In the subjective selection of the stands for this study we attempted to include forest sites across the complete environmental gradient under which trees can grow in interior Alaska. Viereck (1975) had suggested that the vegetation types in interior Alaska were distributed along general gradients of temperature and moisture. This strategy provided an ideal framework within which we could test the central hypothesis of the research program. To characterize this gradient we have used two criteria, a soil degree day (SDD) sum and the average percent moisture in the upper portion of the mineral soil. Figure 3 shows the distribution of the 23 stands along the two axes of this environmental gradient.

The extremes in the environmental gradient run from the aspen stand on a steep bluff (stand 11) with an SDD of 2217 and an average soil moisture of slightly less than 20% to black spruce sites with an SDD as low as 483 and an average soil moisture of 250%. The aspen site is at the lower limit of soil moisture for tree growth in interior Alaska, being adjacent to an *Artemesia*–grassland on the same slope. The cold, wet extreme is represented by a cluster of black spruce stands, all underlain by permafrost and with a shallow active layer. The wettest site is stand 14, an open black spruce stand on a north-facing slope. The coldest site is a lowland open black spruce stand on an old terrace of the Tanana River (stand 20). The treeline site, although having the lowest summer air temperatures (with an air degree day sum of 500), did not have soil temperatures as cold as the wetter sites. In this case air temperatures and wind rather than soil temperatures are probably the limiting factor controlling growth. As hypothesized, the two black spruce stands (stands 33 and 34) at the intensive site at Washington Creek, are close to the cold-wet extreme of the environmental gradient.

Figure 3 shows two circled clusters of stands; the black spruce stands, all with an SDD below 800 and with an average soil moisture above 60%, and the stands on white spruce sites, all with an SDD between 800 and 1400 and with an average soil moisture between 30 and 50%. This mesic group includes the white spruce stands and the broadleaf stands that are successional to white spruce (i.e., aspen, birch, and balsam poplar). Stand 28 (outside the circled area), a mixed white spruce and black spruce stand, is successional on an intermediate aged terrace of the Chena River in transition from white spruce to black spruce (Viereck 1970) but environmentally is still closest to white spruce sites.

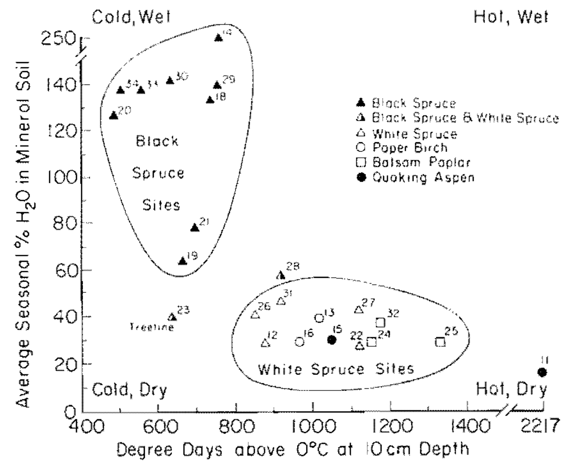

FIG. 3. Location of 21 semi-intensive sites (stands 11–16 and 18–32) and the intensive site (stands 33 and 34) along an environmental gradient determined by accumulated soil degree days and average seasonal moisture in the mineral soil.

The other two stands outside of the circled clusters are the treeline mixed white and black spruce stand site (23) and the aspen stand on a bluff (11).

The cluster of black spruce stands shows a wide range of average soil moisture (65 to 250%) and a narrow range of soil temperatures (450 to 750 SDD). Most of the black spruce stands are underlain by permafrost but three (18, 19, and 21) are not. There is no real difference in the soil temperature regime at 10 cm for the permafrost and permafrost-free sites. Two of the permafrost-free sites (19 and 21), however, one on a ridgetop and the other in a ridge saddle, have significantly better drained soils.

Because of the obvious clustering of the two groups of stands (one cold and wet, the other warm and mesic) and previous recognition of two distinct forest sites in interior Alaska (Foote 1983), we found it useful to characterize and compare these two site types rather than to discuss more subtle differences that may occur along the entire environmental gradient.

Vegetation

In the vegetation tables (Tables 1 and 2) the stands are arranged roughly along the environmental gradient except that they are also grouped by dominant species. For convenience, treeline has been grouped with the mixed white and black spruce stand on the Chena River terrace although environmentally it could be included with the black spruce stands.

Although only a few stands were subjectively selected for this study, some general relationships between individual species and the environmental gradient can be inferred from the vegetation data and from general observations. The general environmental pref-

erence of the six tree species of interior Alaska is indicated by Table 1. Aspen is most common on the warm mesic sites, both in pure stands and with paper birch and white spruce. It is a successional, short-lived species that comes in quickly after wildfire. Although not indicated in our data, aspen is sometimes found as a successional species on the more mesic black spruce sites (Foote 1983).

Balsam poplar is found primarily in floodplain stands where it is dominant and in younger white spruce stands where it is gradually replaced by the spruce. The newly deposited alluvial soils are relatively warm, with SDD ranging from 1150 to 1310.

Paper birch and white spruce both occur over a broad range of environmental conditions. White spruce replaces aspen on all but the driest sites, occupies most of the permafrost-free mesic sites, and is also found in some colder sites, especially those on river terraces and at treeline. Paper birch is also an intermediate species; it is often found following fire in both cold and warm sites. In the uplands it tends to be on cooler slopes than the aspen stands and can occupy cold north-facing slopes where it is successional to black spruce. It is also a minor component in floodplain white spruce stands.

Black spruce is found almost exclusively on the colder sites. With its shallow root system and ability to conserve nutrients, it seems well adapted to growth on the cold sites with a shallow active layer over permafrost. With its semiserotinous cones it tends to replace itself directly after fire on these cold sites. Even on the floodplain, it dominates the older terraces and eventually replaces white spruce as the terraces become elevated above flood level.

Tamarack is of minor importance in interior Alaska, occupying primarily cold, wet sites on old river terraces. It is commonly found in some of the bogs in interior Alaska. In our study it was a minor component of two of the black spruce stands on older river terraces.

From the cover values of the shrub species in the 23 stands (Table 2) some general relationships to the environmental gradient can be seen. Two tall shrubs, *Rosa acicularis* and *Alnus crispa*, are found across almost the entire environmental gradient, both in upland and floodplain stands. *Rosa acicularis* has higher cover values in the mesic stands but occurs in most of the black spruce stands. Alder seems to have about equal cover in both cold and warm sites.

A number of low shrubs are limited to the black spruce stands and the treeline site. These include *Ledum groenlandicum*, *L. decumbens*, *Vaccinium oxycoccus*, and *V. uliginosum*. *Vaccinium vitis-idaea*, the most abundant low shrub in the black spruce stands, also occasionally occurs in white spruce and birch stands. *Betula glandulosa* occurs at the treeline site where it has a cover value of 34%.

Indicators of the mesic sites among the shrubs are limited to *Viburnum edule* and *Linnaea borealis*. *Shepherdia canadensis* and *Arctostaphylos uva-ursi* are abundant at the warmest and driest sites, but do not occur in, or are rare in, the mesic site samples.

Occurrence of herbaceous species is erratic and there are few species that show strong tendencies toward either the cold or the mesic sites. Several are limited to the dry aspen bluff, and a few have limited occurrence in only the black spruce stands. *Calamagrostis canadensis*, *Geocaulon lividum*, and *Cornus canadensis* show a ubiquitous distribution along the gradient. *Equisetum sylvaticum* and *Rubus chamaemorus* are commonly found in the black spruce and mixed white and black spruce stands.

Mosses and lichens tend to show more specific preferences to either the cold or the mesic sites than do most of the vascular species. Both mosses and lichens have low cover values in the hardwood stands. *Hylocomium splendens* is abundant in both black and white spruce stands. *Rhytidiadelphus triquetrus* occurs only in floodplain white spruce stands but is abundant in only one stand. *Pleurozium schreberi*, although occurring in most white spruce stands, is the dominant feather moss in most of the black spruce stands. *Sphagnum* spp. are limited to black spruce on the coldest sites with permafrost. The lichens are found almost exclusively in the black spruce stands; only *Peltigera canina* occurs with any regularity in the white spruce stands.

Tree production

A broad range of tree productivity is encountered along the environmental gradient. Cold, wet soils support an average standing crop of black spruce biomass of 5 $kg \cdot m^{-2}$ compared with average biomass of 17 $kg \cdot m^{-2}$ in white spruce, and 11 to 12 $kg \cdot m^{-2}$ in aspen, birch, and poplar (Table 4). Maximum standing crop biomass ranges between 15 and 25 $kg \cdot m^{-2}$ in the mesic forest types. Within the same age-class (130 years) standing crop biomass in black spruce may range from 5 $kg \cdot m^{-2}$, on permafrost dominated sites, to 11 $kg \cdot m^{-2}$, on permafrost-free sites.

Average annual tree production ranges from about 110 $g \cdot m^{-2} \cdot year^{-1}$ in black spruce to between 366 and 562 $g \cdot m^{-2} \cdot year^{-1}$ in the mesic forest (Fig. 4 and Table 4). Maximum tree production, 952 $g \cdot m^{-2} \cdot year^{-1}$, was measured in balsam poplar stands on the floodplains. Litter fall also follows the same trends, with a low average annual return of 43 $g \cdot m^{-2} \cdot year^{-1}$ for black spruce and a maximum average return of 389 and 251 $g \cdot m^{-2} \cdot year^{-1}$ for balsam poplar and birch, respectively.

Forest communities

The various distribution patterns of individual species along the environmental gradient are reflected

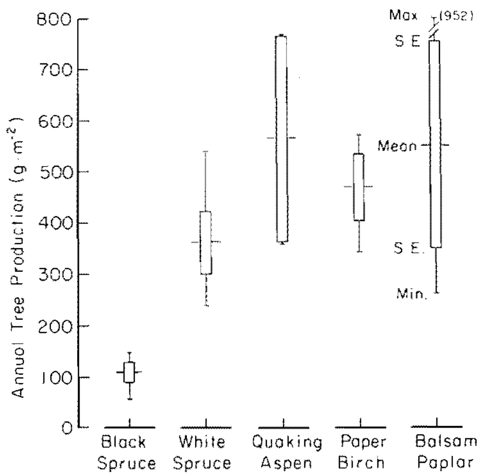

FIG. 4. Annual tree production for five forest types in interior Alaska.

in the changes in forest community types. On the warm and dry sites the two aspen communities are distinct; an open stand with *Shepherdia canadensis* and *Calamagrostis purpurascens* dominating the understory in the warmest, driest site, and a closed aspen stand with *Viburnum edule* and *Linnaea boreale* in the cooler, moister site. The birch stands, on cooler and moister sites than the aspen stands, represent different ages of the same forest type, with *Alnus crispa* and *Calamagrostis canadensis* important species in the shrub and herbaceous layers.

On the floodplain the three balsam poplar stands, although varying in age, were all in the same community type, with *Alnus tenuifolia, Rosa acicularis,* and *Equisetum pratense* the most important shrub and herbaceous species. They reflect a successional relationship more than an environmental one. The white spruce stands on the floodplain show only minor differences from the upland stands in relation to soil temperature and moisture and to forest community types. They are closed conifer types dominated by feather mosses, either *Hylocomium splendens* in the upland or *H. splendens* or *Rhytidiadelphus triquetrus* on the floodplain. In all but one upland stand, *Rosa acicularis* is a characteristic shrub.

The black spruce community types show more diversity. The permafrost-free sites have closed canopy types with a poorly developed shrub layer but with a well-developed feather moss layer, primarily *Pleurozium schreberi*. Toward the cold, wet end of the gradient the canopy becomes more open, with one stand on a steep north-facing slope having only 12% tree cover. Also in stands with more open canopy, *Ledum groenlandicum, Vaccinium uliginosum,* and *V. vitis-idaea* are the characteristic low shrub species. An important characteristic of the black spruce communities on the coldest sites is the dominance of *Sphagnum* spp. and *Cladonia* spp. on the forest floor.

Soils and topography

The parent material underlying the two site types (i.e., the cold, wet sites and the mesic sites) is essentially the same, either loess or river alluvium. The mesic stands of aspen, birch, poplar, and white spruce are found on well-drained uplands or on alluvium that is close to river channels. The black spruce stands are on poorly drained or moderately poorly drained silt loams on older terraces of the rivers or in the uplands on ridgetops or north-facing slopes. Of all the black spruce stands only the two in the intensive site are on a south aspect, but the combination of higher elevation, low slope angle, and midslope position makes this a colder site. The soils on which mesic stands occur are classified Alfic Cryochrepts or Typic Cryofluvent, whereas soils on the permafrost sites are Histic Pergelic Cryaquepts or Pergelic Cryaquepts. The nonpermafrost black spruce sites are classified as Aquic Cryochrepts or Alfic Cryochrepts.

Summary

Forest sites in the taiga of interior Alaska extend over a wide environmental gradient but can be basically divided into the cold, wet, black spruce sites usually underlain by permafrost and mesic white spruce sites, and the successional stages leading to white spruce on warm, well-drained permafrost-free soils. Accumulated SDD range from 2217 at the warmest sites to 480 at the coldest permafrost-dominated sites. Mesic sites range from 800 to 1300 SDD. A moisture gradient in the soil is also present.

Forest types range from successional stands of aspen, balsam poplar, and paper birch on the warm sites, to open black spruce and sphagnum types on the coldest sites. White spruce stands occupy upland and floodplain mesic sites. As would be expected, there are a number of plant species associated with either cold or warm sites and a few species that are ubiquitous on both sites. A larger number of species seems to be limited to the black spruce sites than to the white spruce sites.

Soils range from Alfic Cryochrepts on most of the mesic sites to Histic Pergelic Cryochrepts on the cold sites underlain by permafrost. Soils on the younger terraces of the river floodplains are Typic Cryofluvents. A typical profile for each soil is described.

Standing crop of tree biomass, annual tree production, and litter fall reflect the changing soil temperature and moisture regimes across the environmental gradient. Cold, moist soils support the lowest standing crop of black spruce biomass, the lowest annual tree production, and the lowest vascular plant litter fall.

Average values for these ecosystem parameters may be, respectively, three, five, and nine times greater on mesic forest sites than on black spruce sites.

The data presented in this paper support the basic hypothesis of the taiga black spruce ecosystem study (Van Cleve, Dyrness et al. 1983) (i.e., that black spruce is a nutrient-poor, unproductive forest type). This low productivity is primarily the result of low forest floor and mineral soil temperatures, and high soil moisture content which retard nutrient cycling and mineralization of organic matter. The black spruce ecosystem is near the end of the range of the cold, wet limits of tree growth and also at the low end of forest productivity.

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